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A biofilm micro-community dominated by the diatom *Campylodiscus neofastuosus* (Surirellales) binds detritus used as food source for rare brittle stars endemic to two Bahamian caves

Miriam Steinitz-Kannan[1], Jerry H. Carpenter[1], Mark A. Nienaber[1]

1 *Department of Biological Sciences, Northern Kentucky University, Highland Heights, KY 41099, USA*

Corresponding author: Miriam Steinitz-Kannan (Kannan@nku.edu)

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Abstract

The rare endemic brittle star *Amphicutis stygobita* (Echinodermata: Ophiuroidea: Amphilepididae) is found in Bernier Cave on San Salvador Island in The Bahamas. We report here on the diatom-rich detritus on which the brittle star feeds. The detritus contains a microbial biofilm dominated by a large diatom *Campylodiscus neofastuosus* Ruck & Nakov that thrives in the cave's brackish water. The biofilm diatoms and bacteria produce sticky, carbohydrate-rich, extracellular polymeric substances (EPS) that add to the detritus' nutritional value and help give the detritus a consistency for *A. stygobita* to pull it into its mouth. Of particular interest is that *Campylodiscus neofastuosus* has distinct cell wall features that make efficient use of the limited light in the cave. It appears these morphological adaptations might focus light onto the chloroplasts increasing light capture. Furthermore, large, dark, and highly lobed chloroplasts serve as an additional low-light adaptation. This is a rare instance where efficient photosynthetic activity by diatoms produces a complex biofilm that feeds an endemic cave species population.

Keywords

Amphicutis, anchialine, Bernier Cave, diatom adaptations for low light, epipelic diatoms, EPS, extracellular polymeric substances, Ophiuroidea

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Introduction

Bernier Cave on San Salvador Island in the Bahamas (24°05'37"N, 74°27'15"W) is the type locality for the rare cave brittle star, *Amphicutis stygobita*, described by Pomory, Carpenter and Winter (2011). This was the world's first known cave brittle star and is only found in Bernier Cave and in nearby Lighthouse Cave (Carpenter 2025). It is much more abundant in Bernier Cave; to our knowledge, only two specimens have ever been found in Lighthouse Cave. Although the brittle star population appears to be small, individuals of *A. stygobita* are difficult to find because their small disks (3-4 mm diameter) are filled with brown detritus. Therefore, their populations could be much larger than they seem, as they are camouflaged by the surrounding brown detritus.

In the laboratory *A. stygobita* did not accept food normally eaten by brittle stars but readily consumed detritus collected from the cave that contained diatoms (Carpenter 2016; Carpenter 2025). In 2013 our examination of the diatoms in cave microbial mats (Figs 1, 2D, E) and detritus showed the dominant species to be *Campylodiscus neofastuosus* Ruck & Nakov (Ruck et al. 2016a, 2016b). This species thrives in the cave's brackish water (salinity 14–28 ppt). We collected and studied the organisms in the cave detritus to be used as a food source in the laboratory for the brittle stars. We believe that the main reason the brittle star population does well in this cave is because of the diatom rich detritus it feeds on.

Detritus and epilithic biofilms have been recognized as important energy sources for cave invertebrates (Simon et al. 2003). However, because cave ecosystems are normally light-limited, these are nutritionally poor food sources. This results in low population numbers and slow growth rates of the organisms they support. A cave with a light-filled entrance allowing substantial photosynthesis should be able to support greater biomass including diatoms.

Phototrophic biofilms containing diatoms are not uncommon in caves. They also consist of filamentous and coccoid cyanobacteria, chlorophytes, and other Protista, which are all held together by the extracellular polymeric substances (EPS) they produce (Roldán and Hernández-Mariné 2009). Such biofilms have been studied in caves with artificial lights visited by tourists, where they are referred to as "lampenflora" (Popović et al. 2023). The diatom composition of phototrophic biofilms is reviewed in Falasco et al. 2014 who list 363 species belonging to 82 genera, most of them cosmopolitan in distribution and usually aerophilic. Most recently Winsborough and Sudbury (2024) described seventy diatom taxa from Hall's Cave, a limestone cave in central Texas, USA. Both Falasco et al. (2014) and Winsborough and Sudbury (2024) found mostly very small freshwater species that are highly resistant to desiccation and tolerate low levels of nutrients and high conductivity. The most common genera were *Hantzschia*, *Diadesmis*, *Orthoseira*, *Luticola*, and *Pinnularia* (Falasco et al. 2014) and in Hall's Cave *Nitzschia palmida* (Winsborough and Sudbury 2024). This diatom composition, except for a few genera, is very different from what we found in the detritus of Bernier Cave. There, the dominant diatoms are large *Campylodiscus neofastuosus*. This species is not mentioned in Falasco et al. (2014) or in Winsborough and Sudbury (2024).

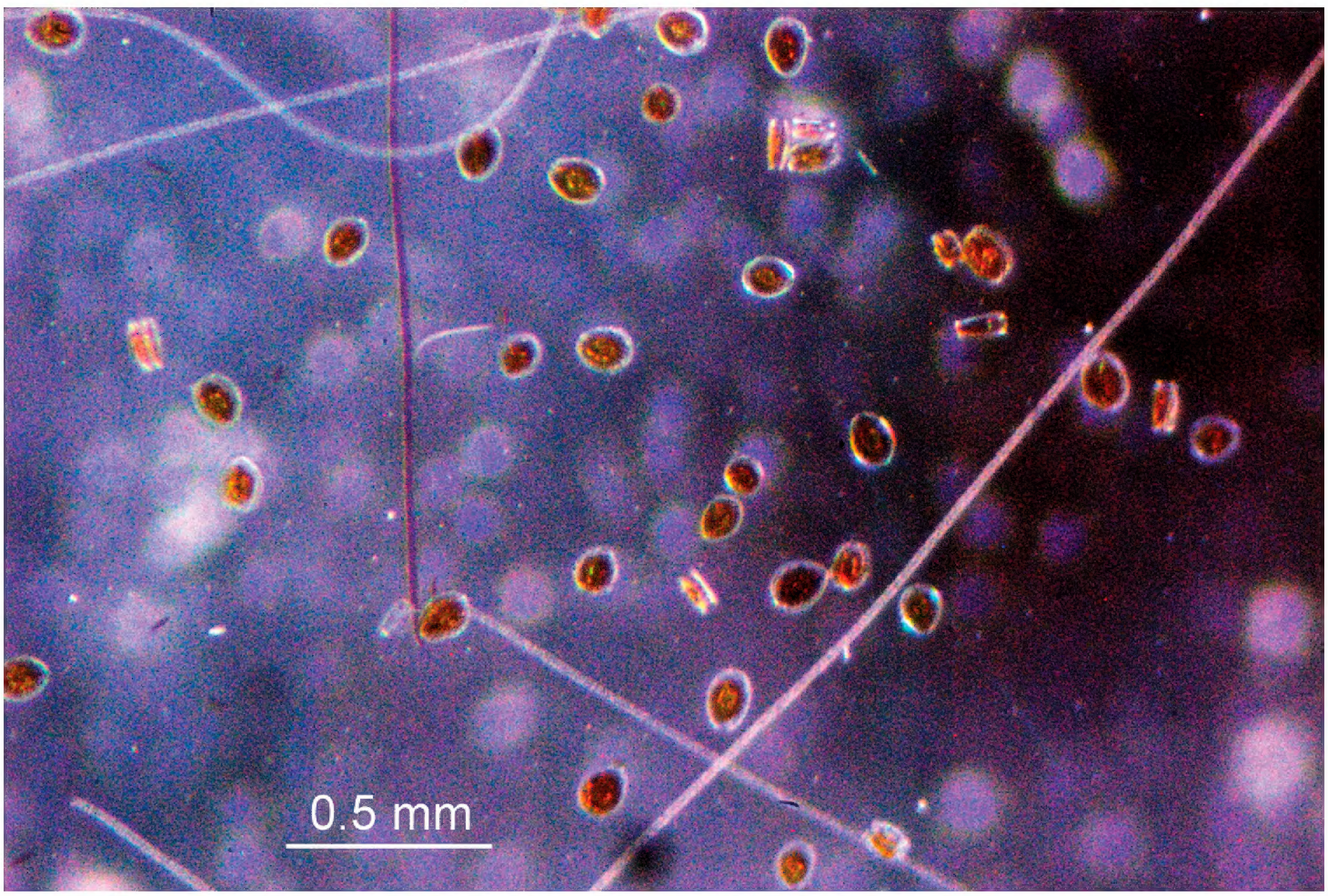

Figure 1. Dissecting microscope view (40X) of microbial mat from entrance room of cave after 9 hours in black film cannister, showing diatoms identified as *Campylodiscus neofastuosus* (from Carpenter 2025).

It is usually found in brackish water and apparently has never been reported from caves. This paper describes this population, its uncommon adaptations to thrive in the low light of the cave, and why it can provide a rich food source for the endemic brittle star.

Materials and methods

Study site

The location of Bernier Cave is described in the companion paper in this issue (Carpenter 2025). One of the most important features of Bernier Cave is that the ceiling entrance is large and directly above or near the water (Fig. 2A). This allows considerable detritus to enter the aquatic ecosystem. It also provides an unusual amount of light to reach the walls of the entrance room to create abundant and colorful growth of algae (Fig. 2B). Water in the cave is brackish with salinities of 14–28 ppt (Carpenter 2025). Tidal fluctuations (changes in water depth between low and high tide) are relatively slight compared to Lighthouse Cave and the ocean water surrounding the island (Fig. 2C). This results in very slow movement of water during tidal flows and allows sizeable accumulations of detritus, some of which is distributed throughout the cave with each tidal flow. The tide line can be seen as a distinctive brown area extending a few centimeters above the water (Fig. 2B, C); we observed that this brown line is a result of prolific

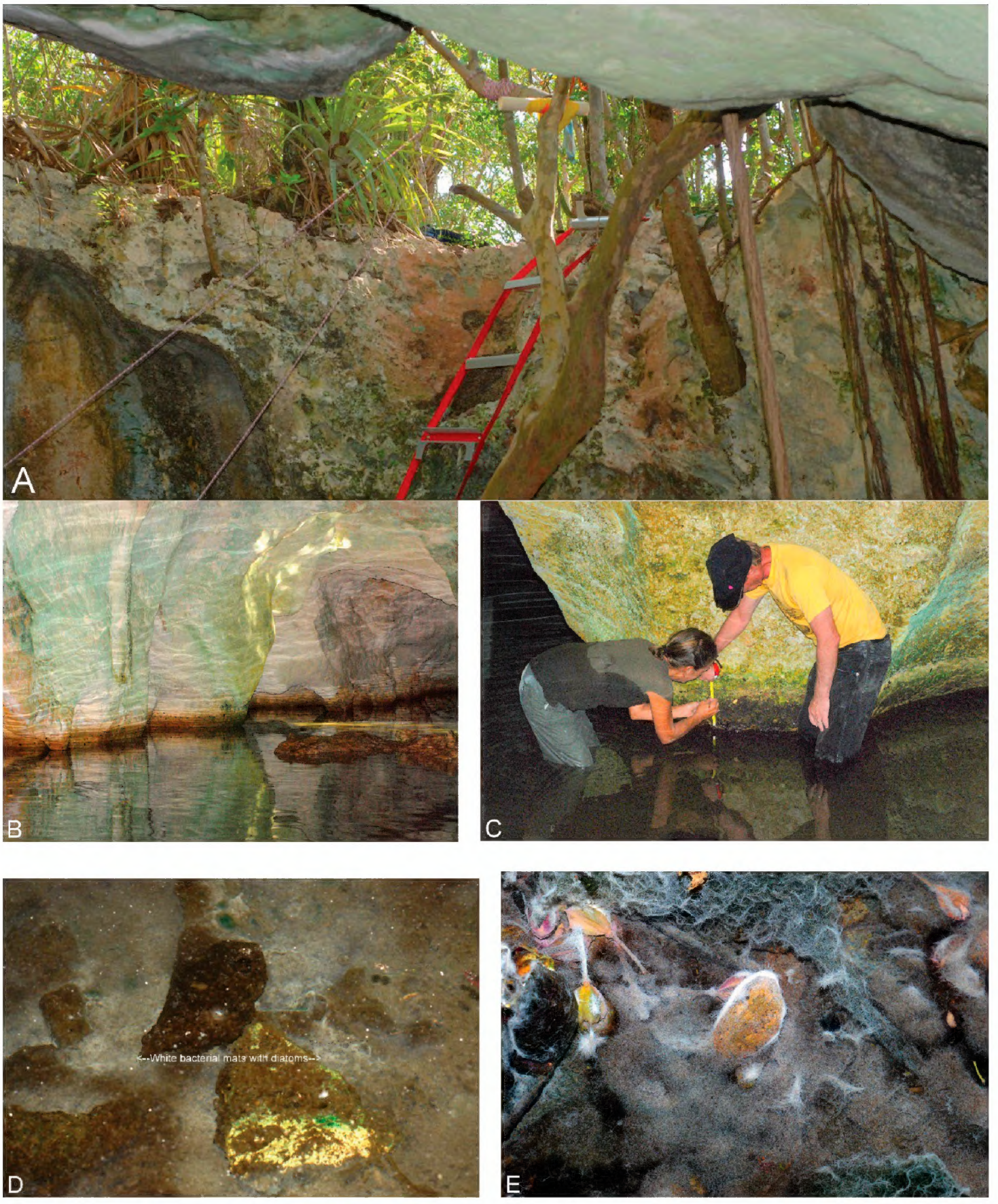

Figure 2. Study site: Bernier Cave, San Salvador Island in The Bahamas (from Carpenter 2025) **A** ceiling entrance **B** algae-covered wall below ceiling entrance **C** tide line composed mostly of *Campylodiscus neofastuosus* in entrance room **D** white bacterial mats in entrance room containing diatoms (brown areas) **E** white bacterial growths on detritus in entrance room.

growth of the diatom *Campylodiscus neofastuosus* and other microbes. The water in the entrance room has a diverse microbial community growing on the walls, the detritus, and in large white mats (Fig. 2D, E). The white mats consisted of filamentous bacteria (mainly *Beggiatoa* and actinomycetes) growing on the organic matter produced, at least in part, by the diatoms seen in Fig. 1.

Collection of detritus with diatoms

In 2013 JHC collected and examined white bacterial mats in Bernier Cave that contained numerous large diatoms (Fig. 1). Samples were given to MSK for identification as described below. Additional collections were made in 2014, 2015, 2016, and 2018 with cave wall scrapings placed in microcentrifuge tubes (Fig. 3B), which were then kept in black film cannisters for later examination and experimentation. In 2015 MSK collected plankton samples (Fig. 3A) and fresh wall scrapings for microscopic examination at the Gerace Research Centre located about 5 km from the cave. Some samples were preserved in Lugol's iodine; these preserved samples and fresh samples (for food for the brittle stars) were brought back to Northern Kentucky University (NKU) for continued study.

Observations of detritus microbial community

All three authors examined detritus samples for composition of diatoms, other microbes, and invertebrates. Detritus was fed to cave brittle stars approximately weekly by JHC (Carpenter 2025). However, adults regenerated very slowly (Carpenter 2016), and babies born in 2018 grew very slowly (Carpenter 2025), possibly because the cave detritus was losing some of its nutritional value as the diatoms in it died. Sköld and Gunnarsson (1996) described the positive effect of diatom supplementation on feeding brittle stars. Therefore, to improve the nutritional quality of the detritus, we experimented with culturing it under different light conditions to try to stimulate the growth of diatoms.

One ml of a well-mixed suspension of cave detritus was placed in standard 6-well tissue culture plates containing 9 ml artificial sea water with salinity adjusted by dilution with distilled water to 30 ppt and 35 ppt. Salinity was measured with a refractometer. Duplicates were made for each plate and identical set ups were kept in (1) an environmental chamber with fluorescent light at 28 °C, (2) a bench next to a lab window at room temperature, and (3) inside a box in the dark at the same room temperature.

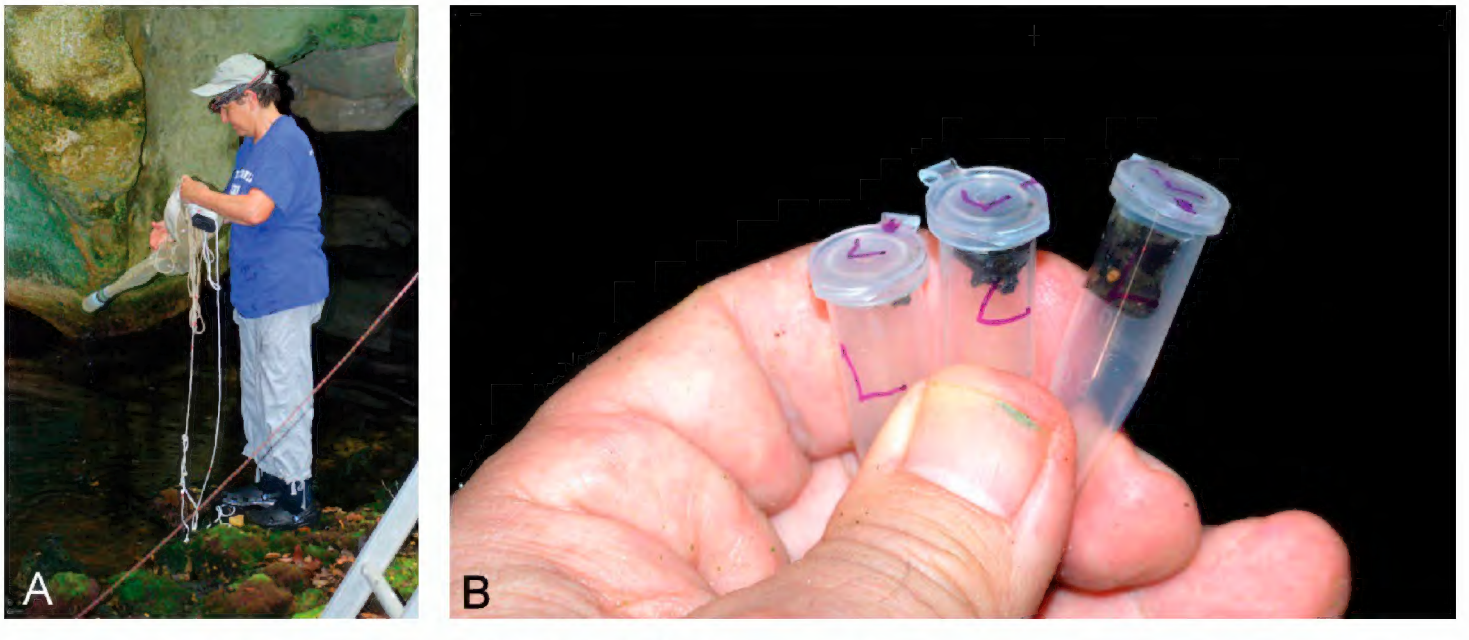

Figure 3. Collection methods **A** MSK with plankton net in Bernier Cave entrance room **B** centrifuge tubes with wall scrapings from entrance room.

Care was taken to ensure *Campylodiscus* frustules were present in each well at the start of the experiment. Plates were examined using a Nikon inverted microscope daily for 6 days noting diversity of species, changes to the initial community, and changes in *Campylodiscus*' chloroplast morphology.

Diatom identification, quantification, and description

For identification purposes, diatoms were examined with an Olympus dissecting microscope, a Nikon inverted microscope, and a Motic compound microscope equipped with a digital camera. SEM images were taken with NKU's FEI Quanta 200 scanning electron microscope. Literature available at the NKU Diatom Herbarium was used to identify the diatoms in our samples. We initially identified the dominant species as *Surirella fastuosa* (Goldman et al. 1990). Regional floras including "Diatoms of Cuba" (Foged 1984) mention this species as commonly found in benthic habitats of brackish ecosystems in the Caribbean. In 2016 *Surirella fastuosa* was renamed *Campylodiscus neofastuosus* Ruck & Nakov (Ruck et al. 2016a, 2016b). Elizabeth Ruck confirmed this identification after examining our cave specimens. Although we did not collect quantitative samples of the detritus, microscopic examination of a well-mixed sample of detritus collected with a plankton net was used to estimate biomass and percentage composition of diatoms.

Results

Detritus as brittle star food

Detritus samples from Bernier Cave were used successfully as food for the brittle stars. Before eating, adult *A. stygobita* usually had central disks that were pale yellow (Fig. 4A) and clear enough to see internal structures such as gonads (Fig. 4B, C). When a few drops of fresh detritus were added to their culture jars, they often started pulling it into the mouth within minutes (Fig. 4B, C) and their disks turned brown (Fig. 4D).

In July 2018 four of the five live adult *A. stygobita* that survived the 6–14 July collecting trip were each observed to contain five to seven broods or gonads inside their disks. On 17 July, one adult released a baby, another was born 31 July, and a third appeared on 6 August. All three babies started consuming detritus when only a few days old (Carpenter 2025). Detritus continued to be their only food source for as long as they lived, which was up to 14.5 months. This feeding behavior drove us to investigate the detritus composition and diversity and to study the chloroplasts and EPS of *Campylodiscus*.

Detritus composition and diversity

Examination of a well-mixed 5 ml sample of detritus under a dissecting microscope at 40X magnification revealed that the detritus micro-community was dominated by *C. neofastuosus.* Observations with a compound microscope at 400X and 1000X

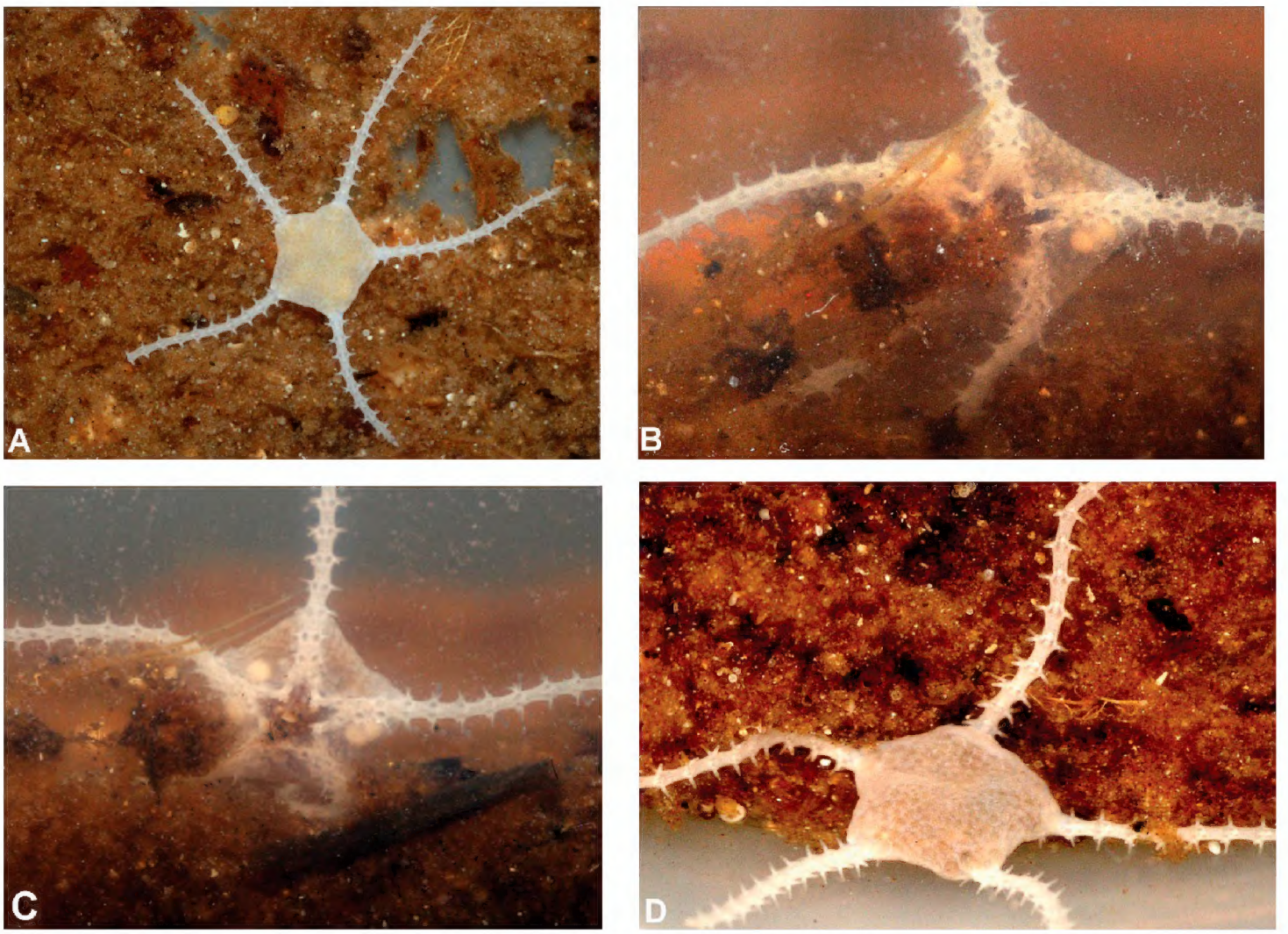

Figure 4. *Amphicutis stygobita* feeding (from Carpenter 2025) **A** light-colored adult with 4mm disk diameter before feeding **B** same animal on side of jar feeding on detritus streaming into mouth **C** same animal, 90 sec. later, with detritus in stomach **D** same animal with brown disk 25 min. after eating detritus.

magnification revealed that other, smaller diatom species were more abundant in the sample, comprising about 70% of all the diatoms. They included the genera *Amphora*, *Achnanthes*, *Achnanthidium*, *Orthoseira*, and *Staurosira* (Fig. 5A–D). In addition to diatoms there were filamentous Chlorophyta, nematodes, ostracods, harpacticoid copepods, ciliates, dinoflagellates, foraminifera, cyanobacteria, and other bacteria. The white mats in Fig. 2D, E consisted mainly of *Beggiatoa*. These are large filamentous sulfur bacteria commonly found in caves (Macalady et al. 2008). However, *C. neofastuosus*, was also abundantly associated with these mats.

Observations of chloroplast morphology under different light conditions

We observed changes in *Campylodiscus* chloroplast shape over the 6-day culture of detritus under various light conditions. In the plates placed in total darkness the chloroplasts filled almost the entire cell. This is just like in the diatoms in the fresh collection from the cave after being kept in black film cannisters for 9 hours (Figs 1, 6A). In the detritus community, kept at low light (close to a window), each chloroplast appeared to be lobed (Fig. 6B). The chloroplasts appear to follow the costae and concentrate pigment in the lens-shaped interior area (Fig. 6C). In the high light treatment group

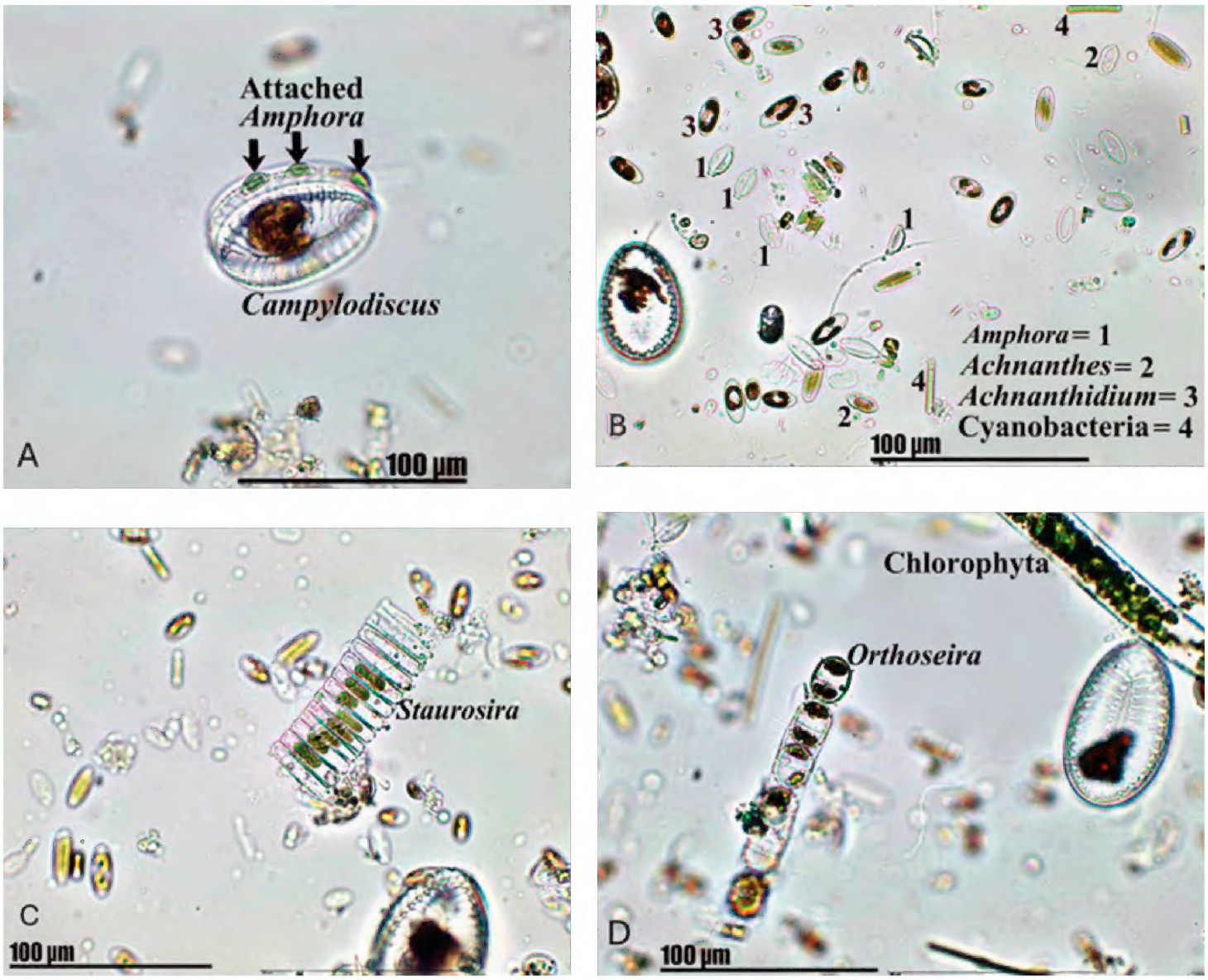

Figure 5. Algae in the detritus collected with a plankton net in Bernier Cave; all images at 400X but identifications were made at 1000X **A** *Campylodiscus neofastuosos* with *Amphora* attached to the girdle band **B** *Amphora*, *Achnanthes*, *Achnanthidium* and Cyanobacteria. Note relative abundance of the very small diatoms **C** *Staurosira* colony **D** *Orthoseira* colony.

(fluorescent light in an environmental chamber) the chloroplasts became compacted around the nucleus (Fig. 6D). No pure cultures of *C. neofastuosus* were attempted. No cultured detritus in this experiment was fed to the brittle stars.

Discussion

Cave environment

As described above, the brown detritus in Bernier Cave that successfully fed *A. stygobita* had an abundance of *C. neofastuosus*. The brown coloration was due partly to the diatom chloroplasts. Samples collected by scraping the brown coloration of the cave walls at the water line (Fig. 3B) were also dominated by this diatom. Several adaptations make C. *neofastuosus* ideal for growing in this specialized niche. There is light in the entrance room of the cave, but it is relatively low light, so we believe that it is the efficient light capturing morphology and chloroplast coloration and shape that make

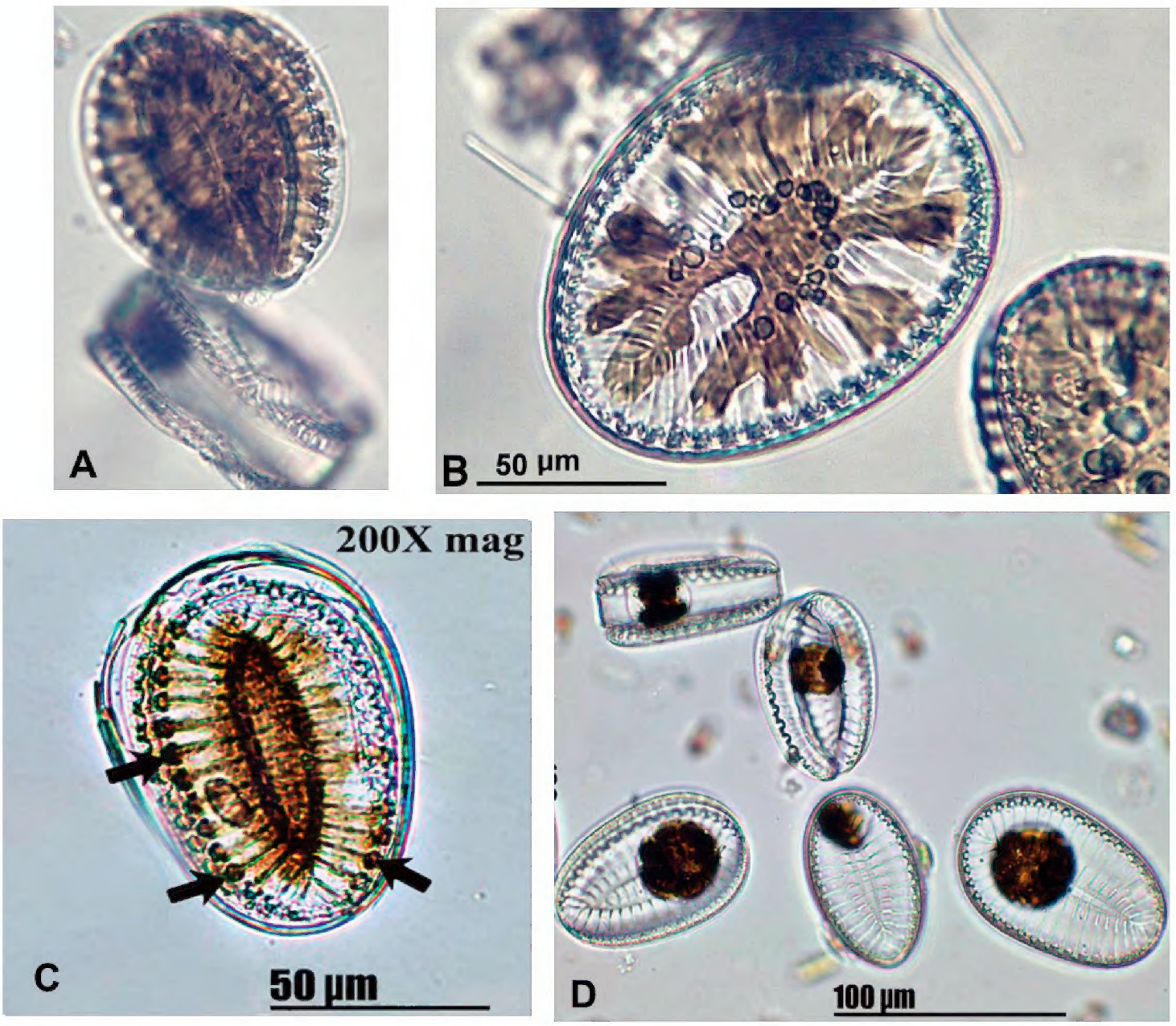

Figure 6. Light micrographs of *Campylodiscus neofastuosus* (100X mag. except for **C**) **A** dark brown chloroplast covering the interior of cell kept in total darkness **B** lobed chloroplast of cells kept in low light **C** chloroplast follows the costae and concentrates in the lens-shaped interior area **D** compact rounded chloroplasts in cells grown in bright light.

the population of *C. neofastuosus* dominate the detritus community found in Bernier Cave. Many diatoms thrive in benthic habitats where light is limited, including species in the genera *Campylodiscus* and *Surirella*. These genera are usually epipelic diatoms, which are diatoms that live attached to sediment particles or at the interface of water and sediment; thus, epipelic diatoms have evolved adaptations to efficiently capture light in such environments (Round et al. 1990). We discuss below specific adaptations that *C. neofastuosus* has for the low-light environment of Bernier Cave.

Chloroplast morphology

The pigments in diatom chloroplasts, particularly the dark brown fucoxanthins, are most efficient at harvesting light and transferring excitation energy to chlorophyll a (Büchel 2020). *Campylodiscus* examined in the field and in preserved samples collected from dimly lit areas of the cave show a lobed very dark chloroplast cover-

ing almost the entire cell (Fig. 6A). Such a chloroplast efficiently collects light. It is composed of mostly fucoxanthin-chlorophyll a/c binding protein constituting the light harvesting complex that transfers photons to chlorophyll a, close to the center of the cell (Scarsini et al. 2019; Büchel 2020). When the detritus was kept close to a window or under a fluorescent light in an environmental chamber the shape of the chloroplast changed. Near the window at low light chloroplasts appeared lobed (Fig. 6B). Fig. 6C shows the chloroplast following the costae that may act as tunnels shuttling photons to the lens-shaped interior area to maximize photosynthesis. With more light the chloroplast became rounder and less lobed and centered around the nucleus, presumably protecting the DNA from UV (Fig. 6D). Such motile or shape-shifting chloroplasts in response to light are common features in diatoms (Mann 1996). Based on chloroplast morphology and cell architecture, *C. neofastuosus* is remarkably adapted to grow in the conditions of Bernier Cave.

Frustule architecture

A distinctive feature of diatoms is the silicon cell wall or frustule. The intricate architecture of the frustule has not only made diatoms famous for their beauty, but its function has been suggested as providing mechanical protection from predators (Hamm et al. 2003), and most importantly providing a devise of efficient light capture (for examples see Goessling et al. 2018, 2021; Ghobara et al. 2019; Svetlana et al. 2022). The optical properties of the frustule have inspired their use in nanotechnology and more specifically in applications in material sciences to produce photonic materials and devices (see for example De Stefano et al. 2007). It is therefore not surprising that a diatom species with remarkable adaptive morphology for more efficient light capture is found in the low light environmental niche of Bernier Cave.

The genus *Campylodiscus* is characterized by valves that are large (76–136 μm long), with the apical axis (Fig. 7A) just slightly longer than the transapical axis. The frustule is usually saddle-shaped, with an elliptical area in the center (Spaulding and Edlund 2009). *Surirella* valves are usually heteropolar, with one rounded end and one pointed end (Spaulding and Edlund 2010). The shape of *C. neofastuosus* as described by Ruck et al. (2016a) and in our collections from Bernier Cave is intermediate between these two forms. Rather than being saddle shaped, it is concave and only slightly heteropolar (Fig. 7A, B). It is shaped like a plano-concave lens consisting of one flat and one inward curved surface (Fig. 7B). This type of lens is ideal for projecting light and expanding the focal length of an optical system (Hradaynath and Singh 2015). The concavity and morphology of the frustule acts as a lens to concentrate the light and focus it onto the lens-shaped central area. The costae (Figs 7A, 8) extend from the margins to the apical axis (Fig. 7A). This diatom has a canal raphe (Figs 7A, 8), well known to enhance motility, allowing the diatom to position itself at an angle best for light capture (Ruck and Theriot 2011). It is also through this canal raphe that the diatom EPS are secreted (Poulsen et al. 2022).

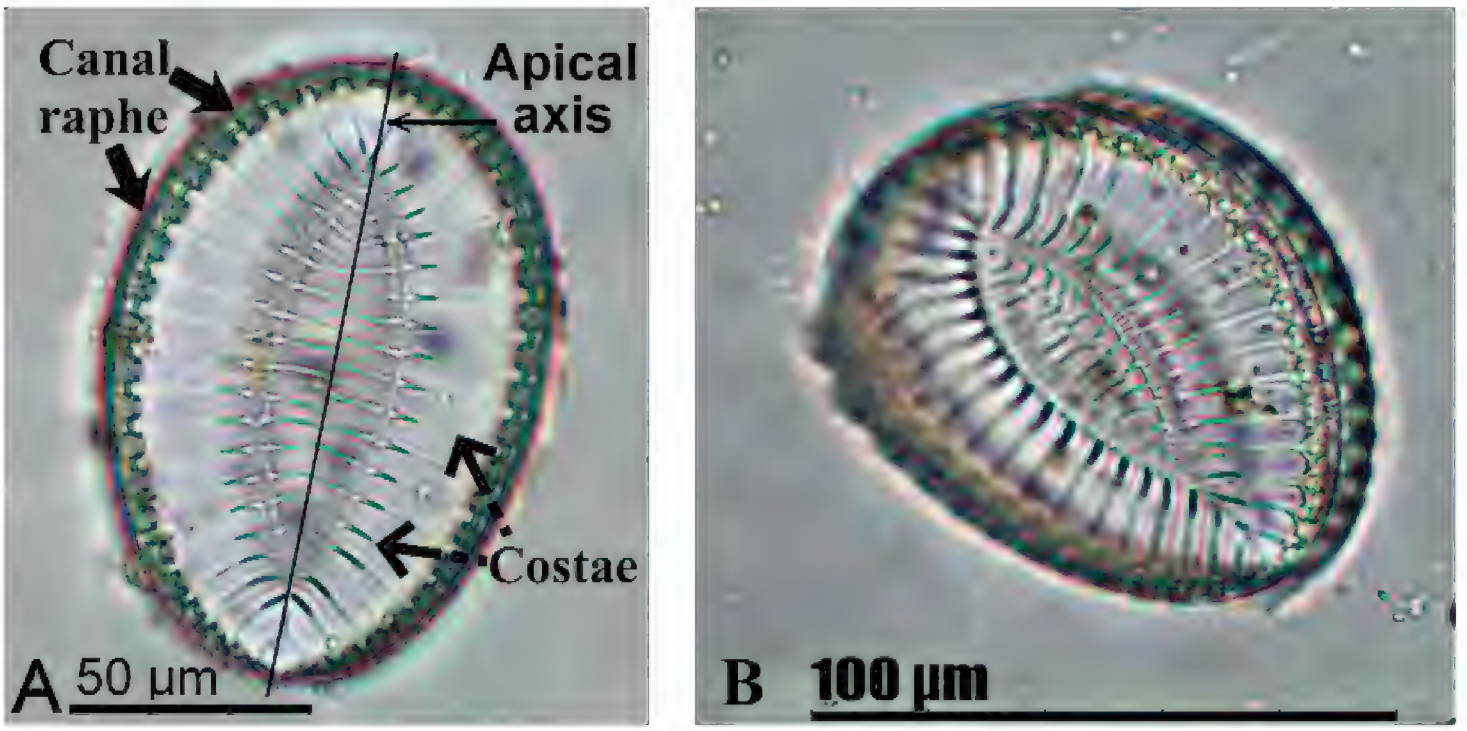

Figure 7. Light micrographs of *Campylodiscus neofastuosus* showing morphology of the valves, including lens-shaped central area **A** shows apical axis in relation to the canal raphe and costae **B** shows concavity of frustule.

Extracellular polymeric substances layer or phycosphere of *C. neofastuosus*

The detritus in Bernier cave is bound by a multi-species microbial biofilm consisting of EPS. Diatom-produced EPS are rich in polysaccharides, monosaccharides and proteins (Zhang et al. 2008). They also contain diatom oils including Omega 3 fatty acids (Oliver et al. 2020). The importance of diatom-produced EPS was not immediately apparent to us when we collected detritus from the cave. However, a recently published book chapter (Underwood 2024) made it clear that the role of EPS as a food source for the cave brittle star should not be ignored. It also called attention to the large amount of literature available on diatom EPS and the need to further study the EPS in Bernier cave.

The EPS layer surrounding diatom cells is known as the diatom phycosphere. The phycosphere is key to symbiotic exchanges where diatom secretions attract a variety of heterotrophic bacteria. These bacteria supply diatoms with nutrients and cofactors essential for their survival. One example is vitamin B12 which diatoms cannot make on their own (Bruckner et al. 2008; Helliwell et al. 2022; Perera et al. 2022). The EPS contributes to the dissolved organic matter (DOM) and particulate organic matter (POM) that are integral parts of food webs in oligotrophic environments (Bhaskar and Bhosle 2006). Our examination of the diatom-rich EPS in the cave detritus revealed a complex microbial community containing, in addition to the diatoms, a diversity of bacteria, protozoans and nematodes. This detritus is likely to be a high-quality food source for *A. stygobita*, just like the energy-rich phycodetritus is for brittle stars in the deep-sea (Ramirez-Llodra et al. 2010).

Abyssal communities feed on diatom-rich biofilm aggregates, called marine snow, that transport nutrients from surface blooms and from resuspension of benthic biofilms (Thornton, 2002). The diatom EPS contributes the stickiness responsible for diatom adhesion to surfaces and to diatom motility (Poulsen et al. 2022), and in doing so, also agglutinates

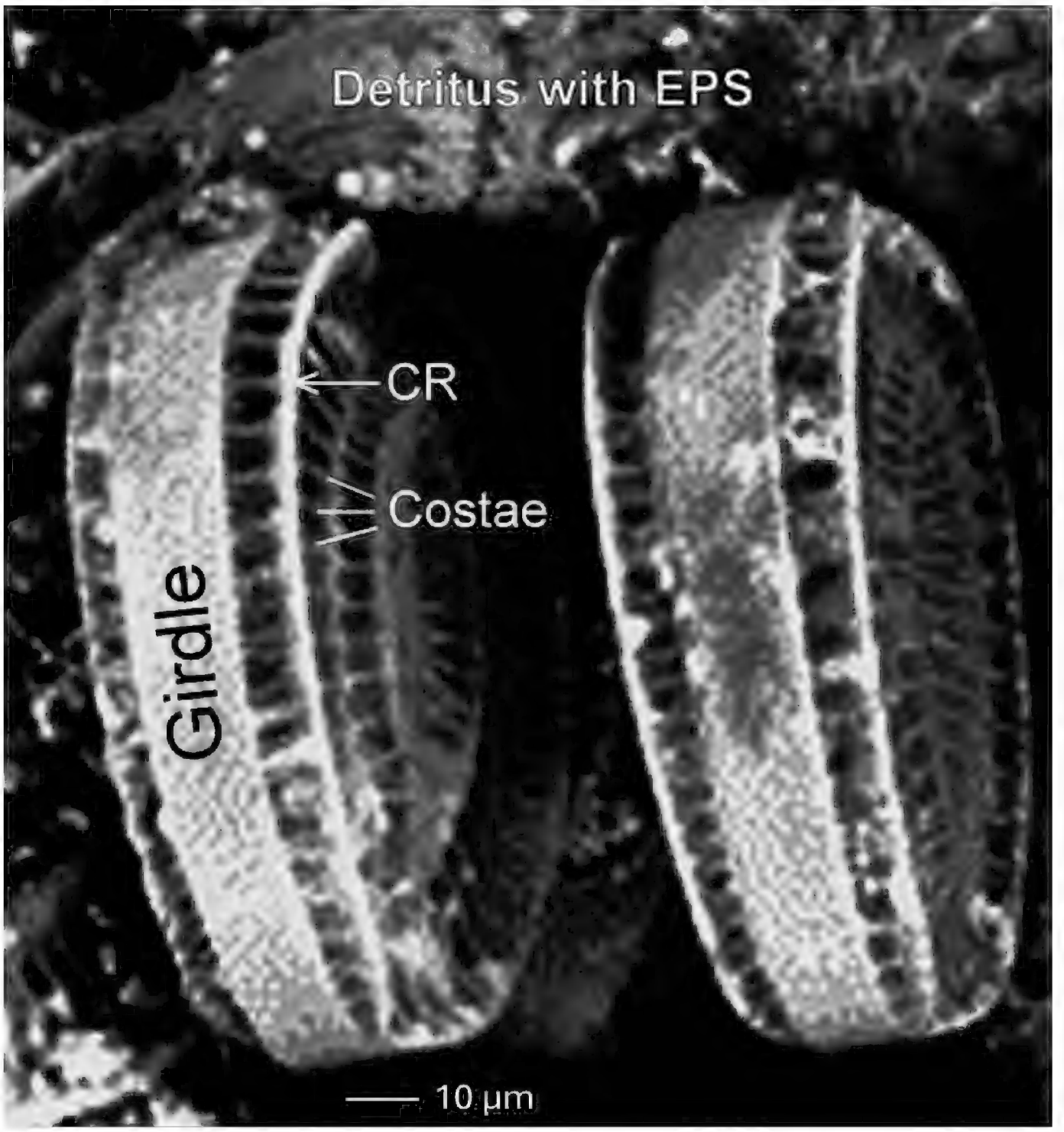

Figure 8. Electron micrograph of *Campylodiscus neofastuosus* from Bernier Cave positioned in girdle view and showing the detritus. Note the fabric-like consistency of the detritus. This is due to it being bound by the extracellular polymeric substances (EPS) secreted from the canal raphe (CR).

particles leading to marine snow aggregates. So, as with marine snow, the diatom EPS in the cave glues together material in the detritus converting it into a loose biofilm easily managed as a food source by the brittle star. The consistency of this loose biofilm is fabric-like (Fig. 8), similar to that described in Heissenberger et al. (1996) for marine snow.

Conclusion

Bernier Cave contains a rare and possibly unique niche that has allowed for the evolution and survival of the endemic brittle star *A. stygobita*. The cave's large ceiling entrance allows both detritus and enough light to reach the walls and water in the

entrance room for microbial communities to thrive. These communities are dominated by large diatoms *Campylodiscus neofastuosus* that have distinct morphological adaptations in their cell wall architecture and chloroplast morphology to make efficient use of the limited light. The diatoms release substantial EPS rich in polysaccharides that bind the detritus (Shnyukova and Zolotariova 2017) and gives it the consistency that allows the brittle star to feed on it. The presence of *C. neofastuosus* makes the detritus in Bernier Cave different from detritus in other caves. These large diatoms enrich and modify the detritus to support a diverse population of detritivores (nematodes, ostracods, copepods, ciliates) and particularly a population of the endemic cave brittle star *Amphicutis stygobita*.

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